REMARKS ON BRAZILIAN DINOSAURS

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To date the dinosaur record in Brazil is limited to saurischians and no confirmed evidence (except probably footprints) of ornithischians is presently known. Two dinosaur taxa were described from the Triassic Santa Maria Formation: *Spondylosoma absconditum* and *Staurikosaurus pricei*. The dinosaurian affinities of *Spondylosoma* are questioned in the literature; *Staurikosaurus* is regarded by some authors as closely related to *Herrerasaurus* from Argentina. No Jurassic dinosaurs are known from Brazil, but there are several Cretaceous occurrences. Titanosaurid sauropods (*Antarctosaurus brasiliensis*, several undescribed postcranials and teeth) and theropods (teeth) are present in the Late Cretaceous strata of the Bauru Group. Spinosaurid theropods have been found in the Albian strata of northeast Brazil and are apparently closely related to some African forms. This distribution pattern may be a product of an Early Cretaceous vicariant event. Spinosaurids as regarded here are not an exclusive Gondwanan group and are also present in Europe (*Baryonyx*). A literal interpretation of the stratigraphic record, therefore, suggests that dinosaur faunal interchanges between Europe and Gondwana may have occurred not only from South to North as previously supposed, but in the opposite direction as well. This hypothesis is very preliminary and can be tested by new and more complete dinosaur material from Brazil and Africa. □ *Brasil, dinosaurs, Triassic, Cretaceous, spinosaurid, soft tissue.*

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Dinosaur remains are recorded from several localities in Brazil (Fig. 1). To date only remains of saurischian dinosaurs are known in this country and no confirmed evidence (except some possibly ichnofossils) of ornithischian taxa have been found (see Campos & Kellner, 1991, for a review). Many specimens have been collected, but most are still undescribed. Apart from the considerable work done on footprints and trackways, (e.g., Leonardi, 1984), little is actually known from the Brazilian dinosaur fauna.

This paper reviews the most important dinosaur occurrences in Brazil, particularly those from the Santa Maria Formation (Triassic), Santana Formation (Early Cretaceous) and Bauru Group (Late Cretaceous). The preliminary description of new specimens (mostly teeth) and the palaeobiogeographic information that can be inferred based on the present knowledge of the Brazilian dinosaurs is also discussed.

SANTA MARIA FORMATION

Triassic dinosaurs in Brazil are only found in the Santa Maria Formation (Parana Basin, south Brazil) which is the most fossiliferous unit of that period in this country. Rhynchosaurs, cynodonts and dicynodonts are frequently found preserved in red sandstones and siltstones. The age of this unit is regarded as ranging from Anisian to Carnian based essentially on the fossil vertebrate assemblages (Barberena et al., 1985).

Two supposed dinosaurs have been reported from the Santa Maria Formation. The first one is *Spondylosoma absconditum* named by Huene (1942) based on some postcranial elements. Colbert (1970) mentioned that two small and compressed teeth with serrated edges may also belong to the same specimen. Romer (1956) listed *Spondylosoma* within Prosauropoda, which was followed by others (e.g., Colbert, 1970). Unfortunately no recent detailed description of this material is available which could provide more evidence about the systematic position of this taxon. According to Sues (1990), the dinosaurian affinity of *Spondylosoma* has not been conclusively presented so far.

A second dinosaur from this unit, *Staurikosaurus pricei*, is only known by the type specimen. This taxon was named by Colbert (1970) on the basis of an incomplete skeleton. Another partial postcranial skeleton found in the Late Triassic Ischigualasto Formation from Argentina was attributed to cf. *Staurikosaurus* sp. (Brinkman & Sues, 1987), but is now referred to *Herrerasaurus* (Novas, 1994).

FIG. 1. Map showing the most important Brazilian dinosaur localities known so far (after Campos & Kellner, 1991). In Rio Grande Do Sul: 1, Santa Maria. In São Paulo: 2, Presidente Bernardes; 3, Adamantina; 4, Pacaembu Paulista; 5, Guararapes; 6, São José do Rio Preto; 7, Ibirá; 8, Colina; 9, Monte Alto. In Minas Gerais: 10, Uberaba/Peirópolis. In Mato Grosso: 11, Morro do Cambambe. In Ceará: 12, Sobradinho; 13, Chapada do Araripe. In Paraíba: 14, Rio do Peixe. In Maranhão: 15, Bacia de São Marcos. In Amazonas: 16, Nova Olinda do Norte.

The phylogenetic position of *Staurikosaurus* has been controversial. In the original description, Colbert (1970) placed this taxon in the Saurischia, regarding it as possibly a carnivorous prosauropod (see Galton, 1977). Benedetto (1973) considered *Staurikosaurus* closely related to *Herrerasaurus* from the Ischigualasto Formation (Argentina) and classified both in the Herrerasauridae, which he excluded from Theropoda. Galton (1973) suggested that *Staurikosaurus* was probably a primitive theropod, but classified this taxon as Saurischia incertae sedis. Later, Galton (1977) placed *Staurikosaurus* in its own higher taxonomic unit (Staurikosauridae), separating the Brazilian species from *Herrerasaurus*, and considered both

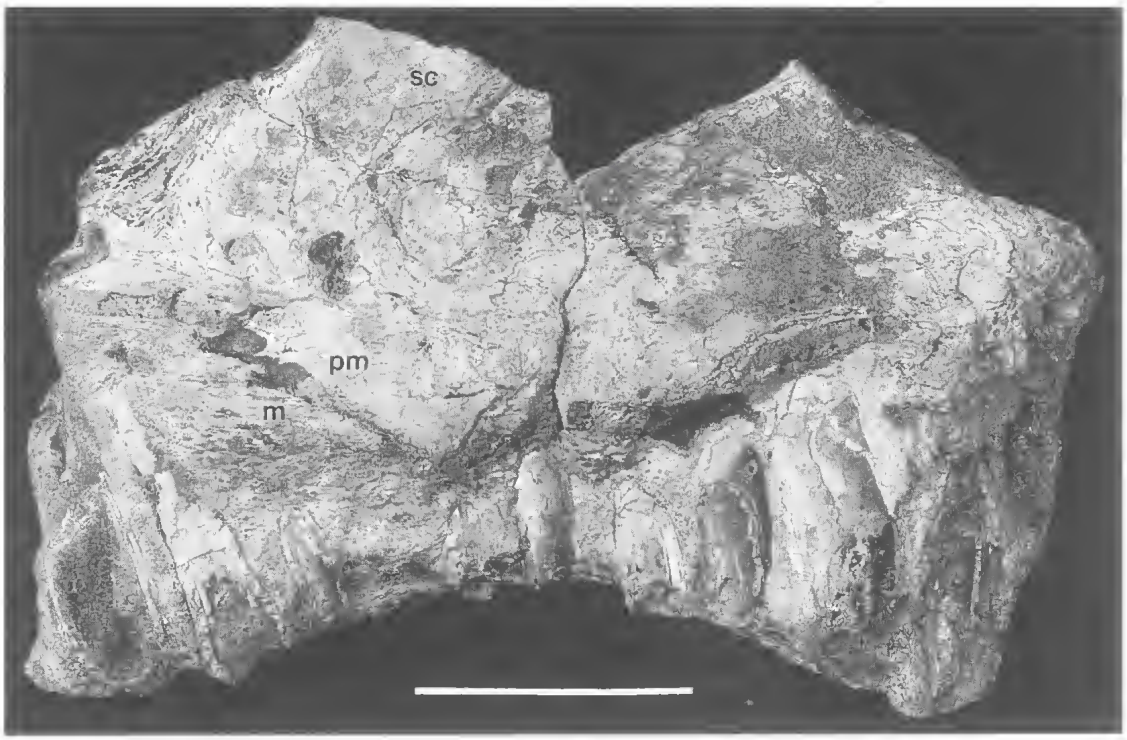


FIG. 2. Brazilian spinosaurid *Angaturama limai*; right lateral view of the anterior portion of the skull (Universidade de São Paulo - USP, São Paulo: GP/2T-5). m=maxilla, pm=premaxilla, sc=sagittal crest; scale = 50mm.

as Saurischia incertae sedis. Brinkman & Sues (1987) also disagreed with the hypothesis of close relationship between *Staurikosaurus* and *Herrerasaurus*, regarding both taxa as successive outgroups for Saurischia + Ornithischia. More recently Novas (1992, 1994) and Sereno & Novas (1992), based on the study of new material of *Herrerasaurus*, suggested that the Argentinean form was closely related to *Staurikosaurus*, and considered both as basal theropods of the monophyletic group Herrerasauridae.

SANTANA FORMATION

The Santana Formation (Araripe Basin, northeast Brazil) is one of the most fossiliferous units in the world. This formation is divided into three members, named from bottom to top: Crato, Ipubi and Romualdo (Beurlen, 1971). According to palynological data (Pons et al., 1990), the age of those strata varies from Aptian-Albian (Crato Member) to middle Albian (Romualdo Member).

The palaeontological content of the Santana Formation is very diverse. The Crato Member is very rich in plants, insects and fishes, but includes pterosaurs (Frey & Martill, 1994; Campos & Kellner, 1996) and birds (so far only feathers). The Romualdo Member is well known for the variety and quantity of fishes, but plants, pterosaurs and crocodilians are also found (see Maisey, 1991). Dinosaur material is rare and presently restricted to the calcareous nodules of the Romualdo Member.

The first dinosaur reported from the Santana Formation is an isolated bone, tentatively identified as an ischium of an ornithischian dinosaur (Leonardi & Borgomanero, 1981). Although probably dinosaurian, the fragmentary nature of this specimen casts doubt about its anatomical identification. This material needs further preparation and at this point should be regarded as Dinosauria incertae sedis.

Another dinosaur specimen reported from the Romualdo Member is the anterior portion of a skull (incomplete premaxilla-maxilla; Figs 2, 3) and represents a new theropod (Kellner, 1994a), *Angaturama limai* (Kellner & Campos, 1996). The rostrum of this dinosaur is very compressed (more than in any other theropod) and the distal portion is expanded ('spoon-shaped'). A sagittal crest formed by the premaxillae is present on the anterior part of the snout. This specimen repre-

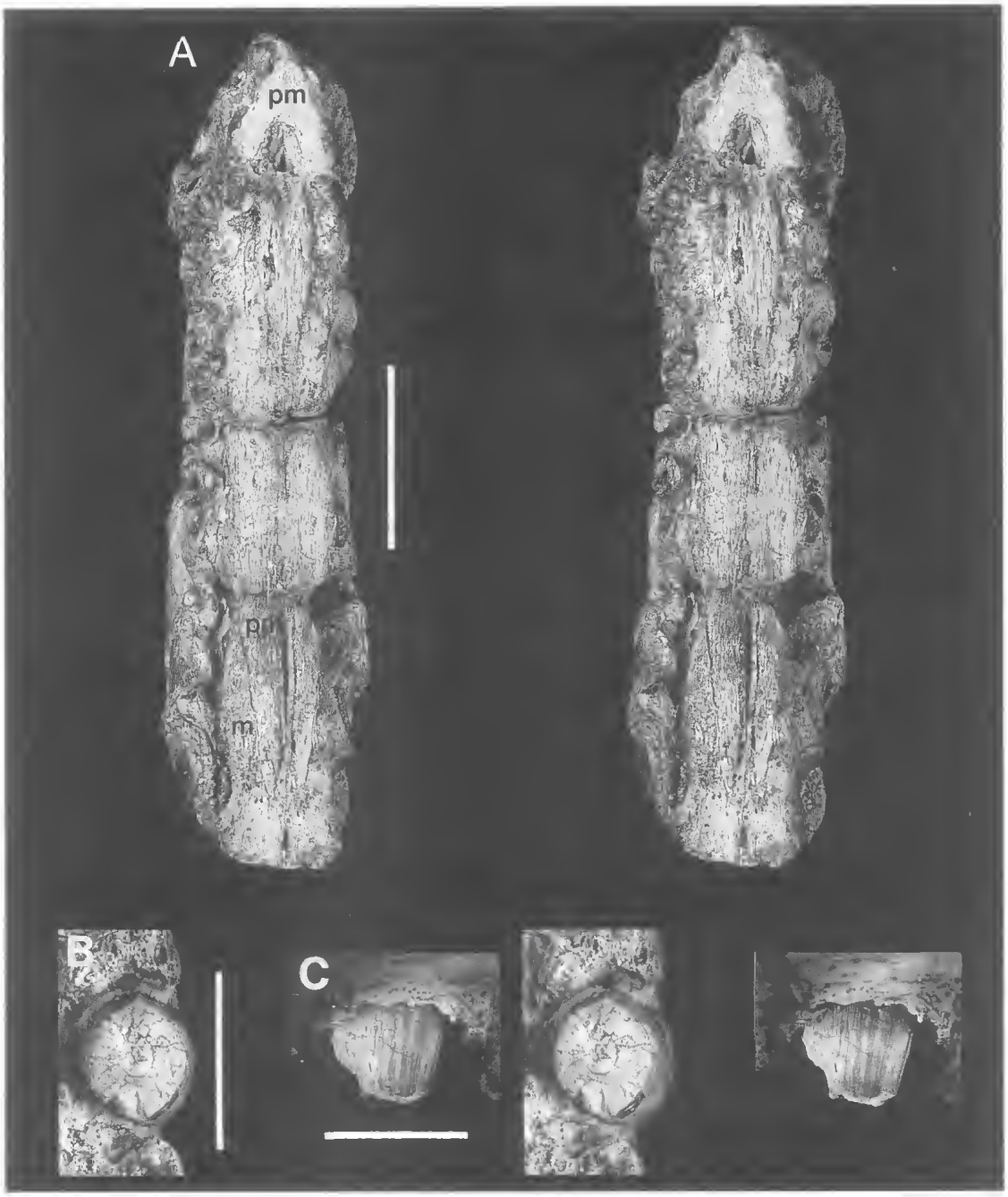


FIG. 3. Spinosaurid *Angaturama limai* (USP GP/2T-5). A, Stereopair of the palatal view. pm=premaxilla; scale = 50mm. B, Right 6th premaxillary tooth, stereopair of the transverse section; scale = 10mm. C, Lingual view; scale = 10mm.

sents the first occurrence of a spinosaurid in Brazil.

Spinosauridae is considered a group of unusual theropods that includes *Spinosaurus aegyptiacus* found in the Cenomanian rocks of Egypt (Stromer, 1915) and the spinosaurids found in Early Cretaceous strata of Gadoufaoua, Niger (Taquet, 1984). *Baryonyx* found in the Barremian

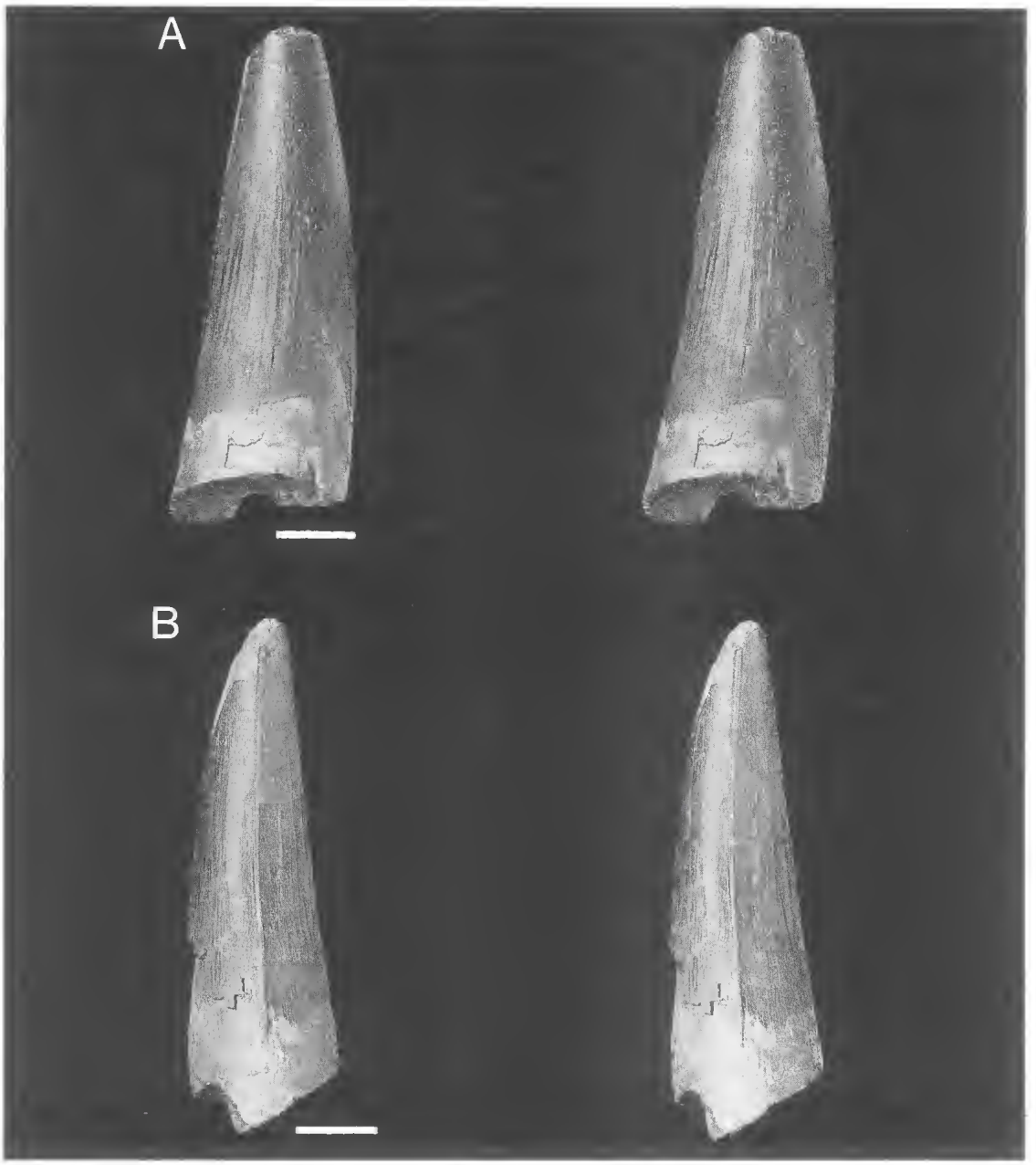


FIG. 4. Isolated spinosaurid tooth from Cretaceous strata of Morocco, housed in the Departamento Nacional da Produção Mineral (DNPM), Rio de Janeiro. A, Stereopair of the lingual view; scale = 10mm. B, Posterior view; note the wear surface on the basal portion of the tooth; scale = 10mm.

of England (Charig & Milner, 1986) is considered a spinosaurid too (Paul, 1988; Buffetaut, 1989a; Kellner, 1994a; Kellner & Campos, 1996; but see Charig & Milner, 1990). Buffetaut (1989a) also attributed to Spinosauridae (*Spinosaurus* cf. *S. aegyptiacus*) a fragmentary maxilla with almost circular alveoli (no teeth were preserved) found in continental red beds of Albian-Cenomanian age in the Taouz region, southern Morocco. More materials from Morocco referable to Spinosauridae are isolated teeth, preserved in reddish sandstone (Fig. 4) that were collected near

the region of Ksar-es Souk (Henry Galiano, pers. comm. 1994) and come possibly from the Tegana Formation (Albian-Cenomanian?). Those teeth are very similar to the ones reported from Albian strata of Southern Tunisia, which are attributed to *Spinosaurus* sp. (Bouaziz et al., 1988).

A potential synapomorphy of Spinosauridae that can be observed in the Brazilian specimen is the 'crocodilian-like' teeth, with subcircular transverse sections and striated enamel. The anterior and posterior keels of the teeth in the Brazilian spinosaurid are unserrated, which is the same condition as in *Spinosaurus aegyptiacus* and the teeth found in Tunisia and Morocco (Fig. 4), but different from the finely serrated teeth in *Baryonyx* (Charig & Milner, 1986; 1990). Other derived characters shared by spinosaurids are: the particular shape of the rostrum (concave ventral margin of the upper jaw, which corresponds to a convex dorsal margin of the lower jaw); the presence of seven premaxillary teeth; and, the external naris displaced backwards (observed in *Baryonyx* and indicated in the specimens found in Gadoufaoua and in Brazil). The last two features cannot be observed in *Spinosaurus aegyptiacus* since the upper jaw of this species remains unknown.

Recently Martill et al. (1996) described another theropod from the Romualdo Member, *Irritator challengeri*, which they regarded as representing a new clade (Irritatoridae) of maniraptoran dinosaurs. The material includes an almost complete skull and mandible which lacks the rostral portion.

Judging from the published picture, this specimen was still unprepared at the time of their study (Martill et al., 1996: 6). It is also not clear if the matrix from several cranial openings has been completely removed or if those openings are only indicated on the picture of the specimen (compare Martill et al., 1996, Figs 2 & 3).

Despite listing several characters that *I. challengeri* apparently shares with different theropods, the authors have not made clear why they regard it as a maniraptoran. The only cranial character used by Gauthier (1986) to diagnose the Maniraptora is the absence or reduction of the prefrontal. The presence or absence of this bone cannot be verified in *I. challengeri* since Martill et al. (1996, Fig. 3) listed this bone but failed to indicate its presence (and consequently its shape and proportions) in the skull. Holtz (1994: 1107), reviewing the phylogeny of theropods, listed as a cranial synapomorphy of maniraptorans the '*jugal expressed on the rim of the antorbital fenestra*'. If the cranial sutures indicated by Martill et al. (1996) are correct, the jugal of *I. challengeri* does not participate in the antorbital fenestra. All other synapomorphies of the Maniraptora are based on postcranial bones (Gauthier, 1986; Holtz, 1994).

Curiously, Martill et al. (1996) did not compare the skull of *I. challengeri* with the spinosaurid, *Angaturama limai*, from the same deposit (Kellner, 1994a; Kellner & Campos, 1996). Nor did Martill et al. (1996) compare their specimen with *Baryonyx* described by Charig & Milner (1986; 1990). They did, however, notice similarities between the dentitions of *I. challengeri* and *Spinosaurus* from Egypt (Stromer, 1915), but pointed out that the '*mandible of Spinosaurus would certainly not fit with the dental margin of the maxilla and premaxilla*' of their material (Martill et al., 1996: 8). It is intriguing how this conclusion was reached, since their specimen lacks the rostral part of the skull.

Preliminary comparison of *I. challengeri* with other spinosaurid taxa indicates that they share at least two synapomorphies: transverse section of the teeth sub-circular and external nares displaced backwards. Those features suggest that *I. challengeri* is a spinosaurid and so there seems no justifiation for the Irritatoridae, here considered a junior synonym of the Spinosauridae.

The comparison of *I. challengeri* with *Angaturama limai* is difficult since they are based on different parts of the skull. Both, however, have unserrated teeth. This feature, associated with the fact that they come from the same deposit, raises the possibility that they represent the same taxon. The preserved posterior portion of the skull of *A. limai*, however, is apparently higher and more laterally compressed than the preserved anterior portion of the skull of *I. challengeri*. Although there is a good possibility that the specimens belong to the same taxon, regarding them as synonymous is premature until more complete material is found.

Another dinosaur specimen from the Santana Formation mentioned in the literature is an incomplete sacrum (Frey & Martill, 1995). The material, only partially prepared, was attributed to a possible oviraptorosaurid on the basis of the presence of pleurocoels. Since oviraptorosaurids are a highly specialised group of theropods whose presence has only definitely been recorded from North America and Asia (Barsbold et al., 1993), the assignment of this incomplete material to this group should be viewed with caution, as indeed was pointed out by Frey & Martill (1995).

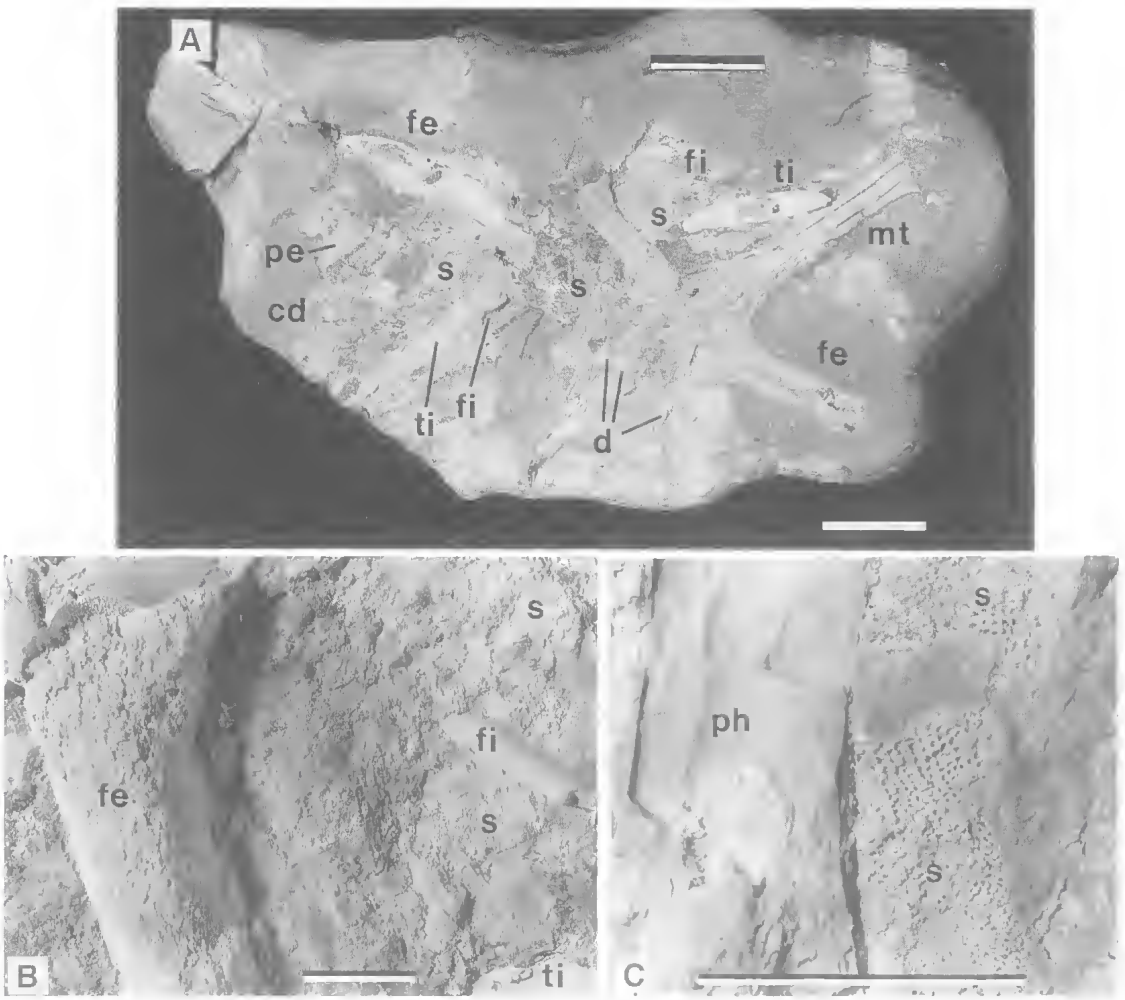


FIG. 5. Small theropod from the Santana Formation, Araripe Basin (MCT 1502-R). A, Complete nodule; scale = 50mm. B, Detail of soft tissue between femur, tibia and fibula; scale = 10mm. C, Detail of soft tissue near one pedal phalanx; scale = 10mm. cd=caudal vertebrae, d=digits of pes, fe=femur, fi=fibula, mt=metatarsals, pe=remains of pelvis, ph=phalanx of pes, s=soft tissue, ti=tibia.

Further dinosaur material from the Santana Formation includes limb bones, one series of nine vertebrae (three sacrals and six caudals), and a complete pelvis with articulated posterior limb elements and several vertebrae (dorsal, sacral and caudal). Recently a calcareous nodule containing both hindlimbs, partial pelvis and several vertebrae of a small theropod (length of femur approximately 175mm) was found (Figs 5, 6). This specimen is particularly striking because of the soft tissue associated with many bones. Since epidermis and muscle fibers are preserved in three dimensions, this might be the best fossilised soft tissue of a dinosaur known so far (Kellner, 1996). Furthermore, longitudinal and transverse sections through a fragment of one femur showed the presence of rod-like structures filling the channels for blood vessels. These structures might be either mineralisations filling those channels or they could represent the replacement of the actual blood vessels. All this material is currently being prepared and will be described elsewhere.

BAURU GROUP

The Bauru Group comprises one of the most extensive continental sedimentary sequences in South America. Outcrops of this unit are found in many Brazilian States (Parana, São Paulo, Minas Gerais, Goiás and Mato Grosso do Sul) and ex-

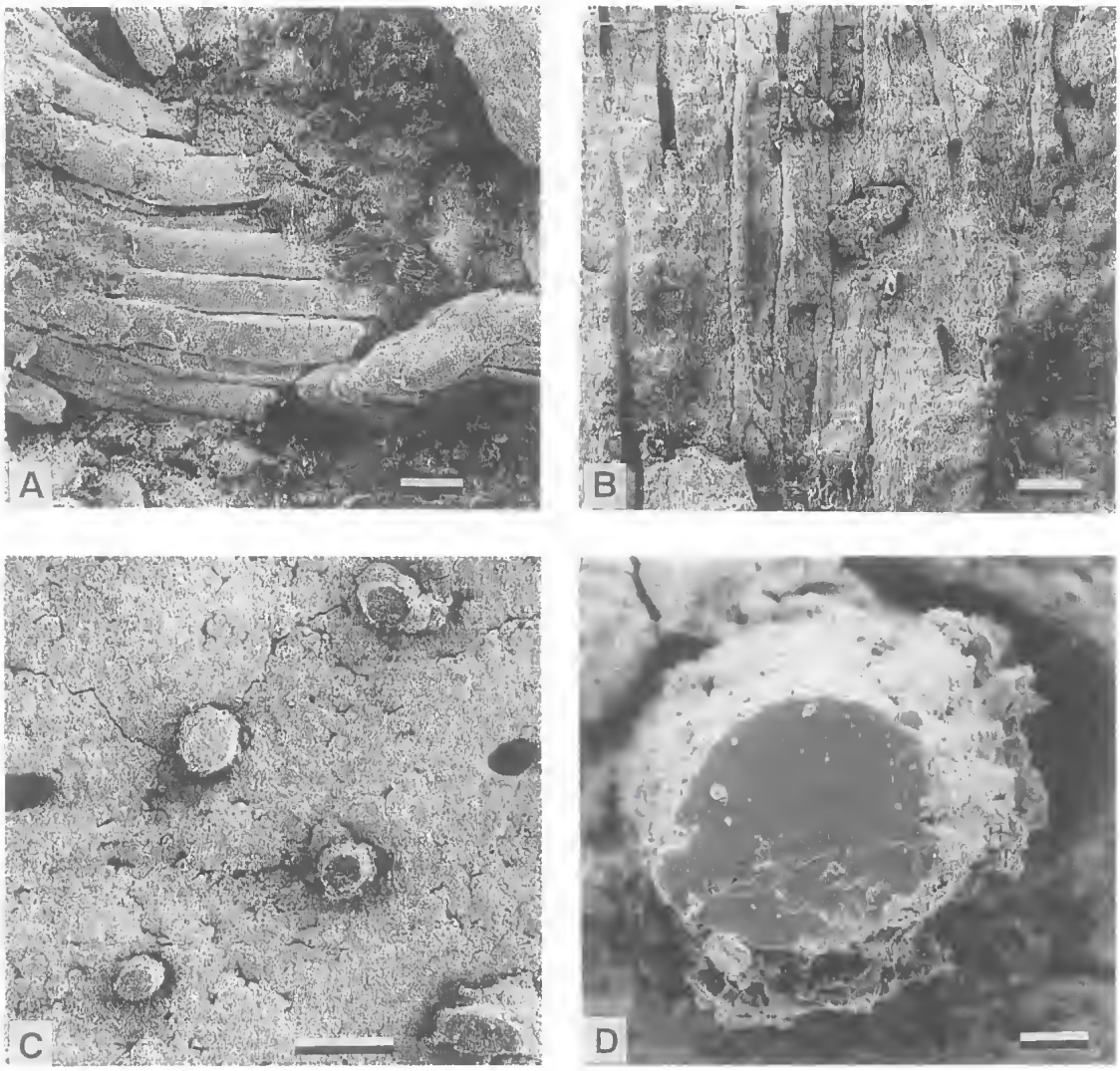


FIG. 6. Scanning electron micrographs of soft tissue preserved in the small theropod (MCT 1502-R) from the Santana Formation. A, Muscle fibres; scale = 50μm. B, Longitudinal section through a fragment of the femur showing rod-like structures preserved in the channels for the capillary blood vessels of the bone; scale = 100μm; C, Transverse section through the same bone showing the rod-like structures; scale = 50μm; D, Detail of one of the rod-like structures; scale = 5μm.

tend into Paraguay. The most widely accepted stratigraphic subdivision for those strata was proposed by Soares et al. (1980), who recognised four formations: Caiuá, Santo Anastácio, Adamantina and Marília. To these, Souza (1984) included the Uberaba Formation, which is interdigitated with the Adamantina Formation. Essentially all these stratigraphical units are composed by sandstones and siltstones, deposited in a semi-arid environment by a meandering river system, and all are of Late Cretaceous age. Among the fossil vertebrates reported are crocodilians, dinosaurs, turtles and fishes, most of which came from the upper layers (Adamantina/Uberaba, Marília formations).

Although dinosaur remains from the Bauru strata were reported at the beginning of this century (Ihering, 1911) and more specimens were collected since, very little is known about the dinosaurian fauna of this unit. A few incomplete specimens were assigned to European and North American taxa, which may be erroneous (Cam-

pos & Kellner, 1991). The only new species described is the sauropod *Antarctosaurus brasiliensis*, based on very fragmentary material (incomplete humerus, femur and dorsal vertebra) collected in São Paulo (Arid & Vizotto, 1971). *Antarctosaurus* was first reported in Cretaceous sediments of Argentina and regarded as a titanosaurid (Huene, 1929; McIntosh, 1990a). More recently, based on the jaw morphology, Jacobs et al. (1993) questioned the titanosaurid affinities of the Argentinean genus, and regarded *Antarctosaurus* as a diplodocid. Due to the fragmentary nature of the material referred to *Antarctosaurus brasiliensis*, there is no particular feature that would support any particular generic affinity of the Brazilian species.

Recently Bertin et al. (1993) reported the presence of an incomplete upper jaw and one tooth referred to Abelisauridae, and an incomplete dentary of a coelurosaur. These potentially important specimens, however, were not described or figured and no diagnostic feature was presented that could support their assignment. The presence of an abelisaur in the Bauru group would be of considerable interest for the palaeobiogeography, since Abelisauridae are considered to have a Gondwanan distribution (Bonaparte & Novas, 1985).

Most of the dinosaur collecting in the Bauru strata was done by Llewellyn Ivor Price near Uberaba and Peirópolis in Minas Gerais where an ongoing excavation is currently being carried out (Campos, 1993). The work resulted in an extensive collection of postcranial dinosaur material which has yet to be described.

The most common dinosaur remains found near Peiropolis are sauropod and theropod teeth (Kellner, 1994b). The sauropod teeth are typically pencil-like: long, slender and subcircular in cross-section. The labial side is slightly more inflated than the lingual side. The enamel has a brownish colour and a rough surface (Fig. 7). Small, unserrated carinae can be observed in well preserved specimens, although in most they are absent (possibly worn down). In some teeth the enamel is almost completely lost, exposing the dentine that has a light color and a smooth surface. Wear surfaces are present and vary possibly according to the tooth's position in the jaw and its age. Based on wear surfaces, the following tooth classes have been recognised:

1) teeth with wear surfaces present on the lingual side and either absent or very limited on the labial side (Figs 7D-F);

2) teeth with wear surfaces present on the lingual and labial side (Figs 7A-C);

3) teeth with wear surfaces present on different parts of the tooth.

Most teeth are of class two, with the lingual wear surface always more developed than the labial one. Some teeth exhibit a combination of wear surfaces (class three), most on the labial and lateral side of the tooth.

The curvature of the teeth changes from almost straight to slightly curved. This variation may also be related to the tooth's position in the jaw. The roots of the teeth can be distinguished from the enamel by their smooth texture and white color. All roots are very small, suggesting that most of the preserved teeth were replaced during the animal's life.

The pencil-like shaped teeth are typical of two sauropod groups: Titanosauridae and Diplodocidae (McIntosh, 1990a, 1990b). Since all sauropod postcranial bones so far reported from the Bauru strata (no skull material is known from this unit) are typical of titanosaurids (e.g., Powell, 1987; Kellner & Borgomanero, 1989), I assume that the teeth described here belong to this group.

There is, however, some morphological variation regarding tooth morphology in titanosaurids. The teeth from the Bauru strata are very similar to those reported by Kues et al. (1980) in *Alamosaurus*, but both differ from the ones described in *Malawisaurus* which, according to Jacobs et al. (1993), are more flattened labial-lingually.

As far as tooth morphology can suggest, there is no evidence of more than one titanosaurid sauropod taxa in the Bauru Group. There are two almost complete pelves, however, of different morphology that indicate the presence of at least two sauropod taxa. The same applies to postcranial elements, all collected in Minas Gerais (Campos, 1993).

Theropod teeth are found in greater abundance than sauropod ones. There are several teeth with distinct morphologies among the material collected near Peirópolis, which range from large blade-like, symmetrical teeth to small, inflated and asymmetrical teeth (Figs 8, 9). The carinae are always serrated, although their configuration might change according to the position of the tooth in the jaw and its age. In one tooth, the middle portion of the posterior carina follows a sigmoid curve (Figs 9A-B), which might have been pathological. Another tooth has a split anterior carina (Figs 9C-D). Split carinae were recently observed in tyrannosaurids (Erickson, 1995) and in one theropod tooth from the Fruit-

land Formation of the San Juan Basin, housed in the New Mexico Museum of Natural History, Albuquerque (NMMNH P-25068; pers. observ.).

The potential for identifying theropods at different taxonomic levels using the morphology of the teeth was already demonstrated elsewhere (e.g., Currie et al., 1990), and is certainly worth investigating in the Bauru material. In a preliminary study of the theropod teeth found in the region of Peirópolis, Kellner (1995) identified six categories:

1) teeth very compressed laterally (blade-like); anterior margin curved distally and posterior margin straight; anterior and posterior carinae with 3 (base) and 2.5 (tip) denticles per mm; denticles straight, longer than wide, and chisel-like (Figs 8C-D);

2) teeth similar to those of category 1 but less compressed laterally; anterior and posterior carinae with 3 (base) and 2 (tip) denticles per mm; denticles straight, longer than wide, and slightly hooked on the basal part of the crown (Figs 9A-B);

3) teeth curved labial-lingually with oval cross-section at the base; anterior carina with 2-3 denticles per mm and posterior with 2.5 (base) to 1.5 (tip) denticles per mm; denticles on posterior carina larger than on anterior; denticles straight, tend to be wider towards the tip of the crown, and are proportionately longer than in categories 1 and 2, but smaller than in categories 5 and 6 (not figured);

4) very similar to those of category 3, but with split anterior carina (only one specimen, Figs 9C-D);

5) recurved and laterally compressed teeth smaller than in category 1; anterior carina with 3 denticles per mm and posterior with 3-4 denticles per mm; denticles on posterior carina larger than those on anterior; denticles pointed, inclined and hooked; blood grooves extend from between the bases of adjacent denticles onto the surface of the crown, particularly on the posterior basal portion (not figured);

6) slightly recurved teeth with labial portion inflated and lingual portion flattened; basal cross-section oval to sub-circular; carinae with 2 denticles per mm; denticles on posterior carina larger than on anterior; denticles inclined, hooked, and wider than those of category 5 (Figs 8A-B).

Based on their morphologies Kellner (1995) suggested that the teeth described in categories 1, 3, 5 and probably 6, represent different theropod taxa, unless the theropods in this unit present accentuated heterodonty. The finding of complete theropod jaws from those layers is needed to confirm this hypothesis.

Other dinosaur remains reported from the Bauru strata include eggs. The first was described by Price (1951) and regarded as belonging to a sauropod dinosaur. The material is not very well preserved and only the impression of the inner portion of the egg shell can be identified in some parts of the specimen.

Further dinosaur eggs were reported by Campos & Bertini (1985) and referred to Ceratopsia (Ornithischia) because of their general similar shape with those found in the Cretaceous rocks of the Gobi Desert, Mongolia. Recently, Norell et al. (1994) have found theropod remains associated with eggs very similar to ones previously attributed to Ceratopsia in a new locality of the Gobi Desert. This raises the possibility that the eggs reported by Campos & Bertini (1985) also belong to theropods.

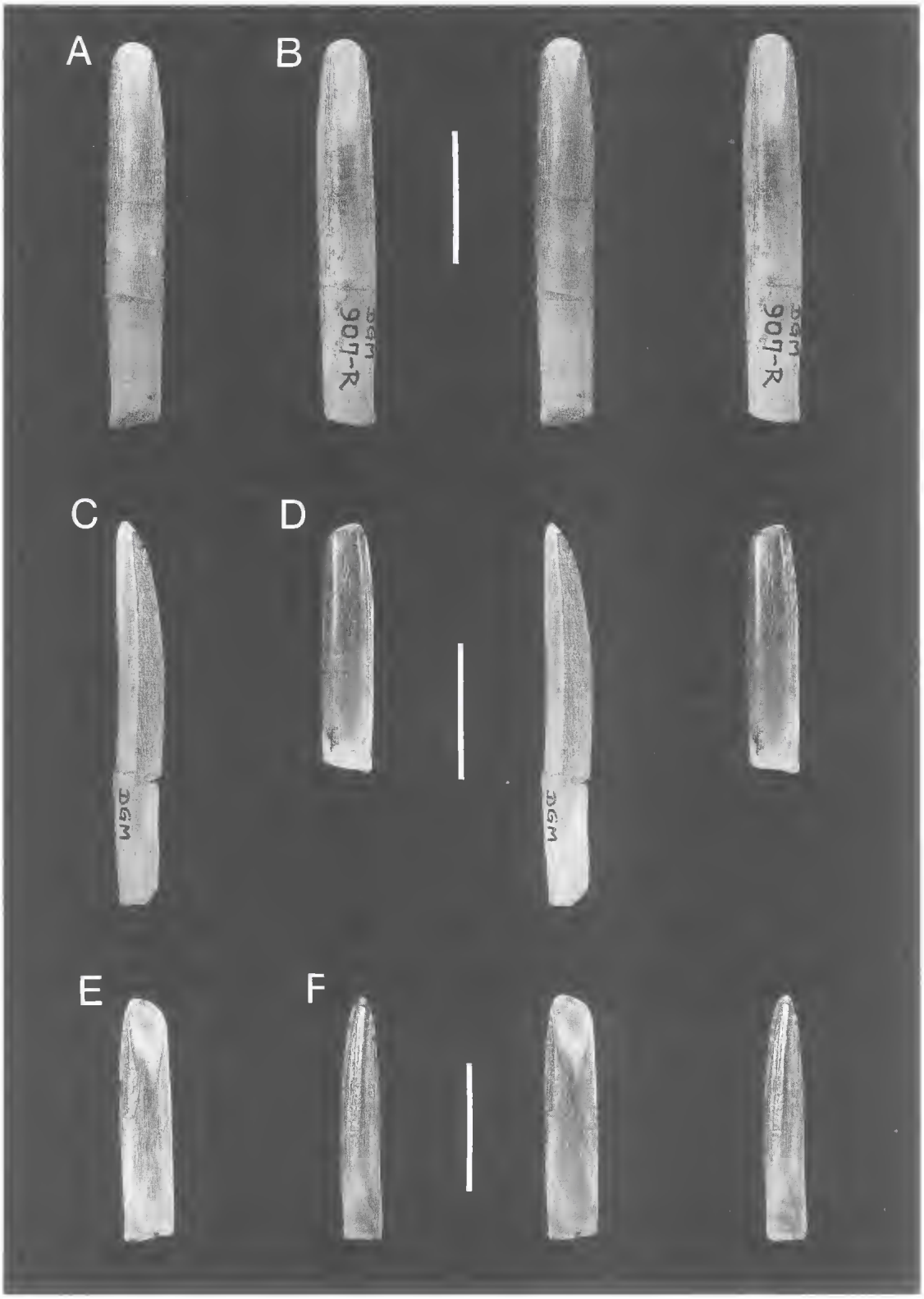
Until detailed descriptions and comparisons of the fossil eggs found in the Bauru strata are available, including an analysis of the microstructure of the egg shell — which may or may not turn out to be of systematic value — those specimens should only be considered Dinosauria incertae sedis.

DISCUSSION

Mesozoic sedimentary strata, especially of Cretaceous age, are well represented in Brazil and provide a high potential for the preservation of dinosaur remains. Despite this fact very few specimens have been recovered, reflecting the lack of collected fossils in this country. This limited information on the Brazilian dinosaur faunas seriously restricts our knowledge of dinosaur diversity and distribution in this part of South America. Nevertheless, the few studies done so far allow some preliminary considerations.

The dinosaurian affinities of the Triassic *Spondylosoma* are not clear (Sues, 1990). *Staurikosaurus*, the other Brazilian dinosaur of that period, is now regarded as a primitive theropod

FIG. 7. A-C, Titanosaurid tooth from the upper portion of the Late Cretaceous Bauru group. A, Stereopair of the labial view; note wear surface. B, Lingual view; note wear surface. C, Lateral view. D-F, Smaller titanosaurid tooth from the upper portion of the Late Cretaceous Bauru group. D, Stereopair of the labial view; almost no wear surface. E, Lingual view; note wear surface. F, Lateral view. Scale = 10 mm.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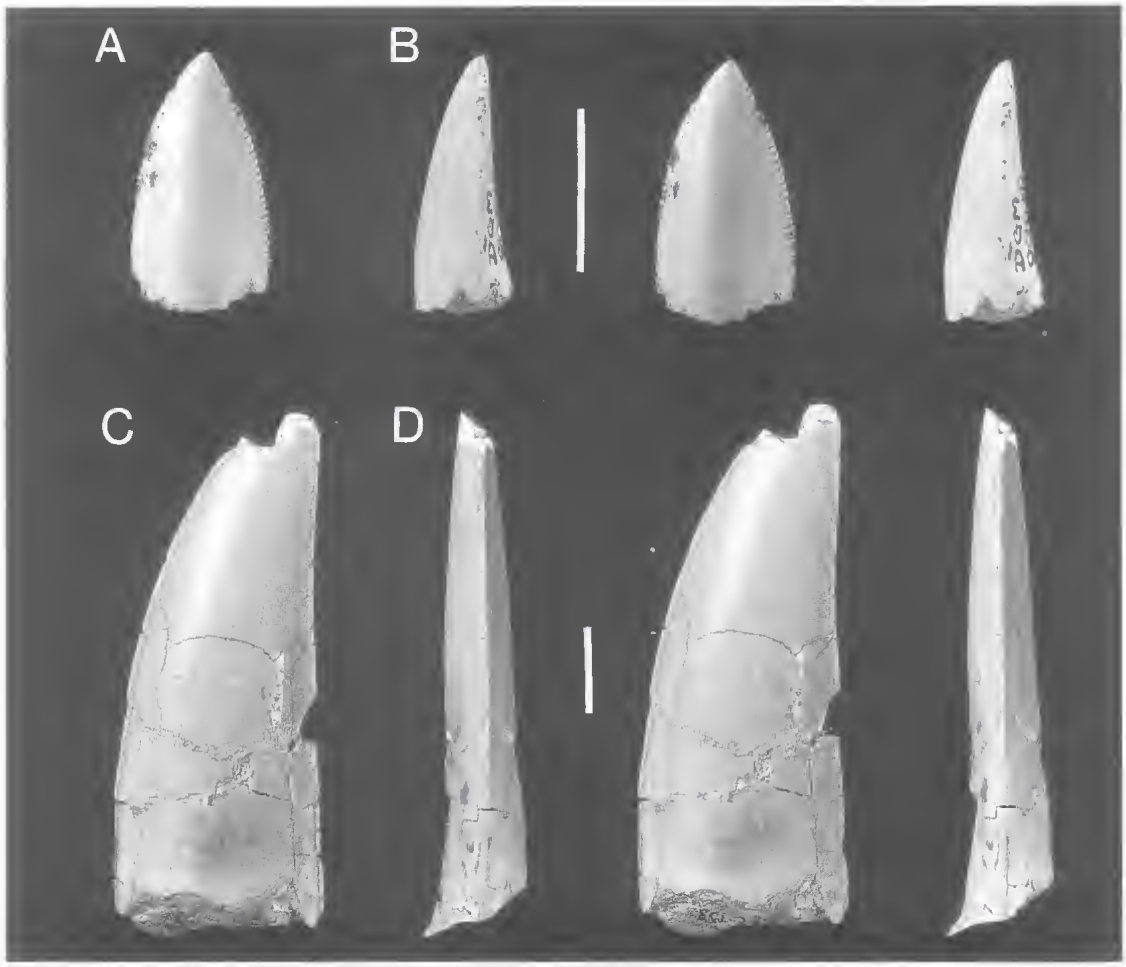

FIG. 8. A-B, Theropod tooth from the upper portion of the Late Cretaceous Bauru group. A, Stereopair of the labial view. B, Posterior view; scale = 10mm. C-D, Large theropod tooth from the upper portion of the Late Cretaceous Bauru group. C, Stereopair of the lingual view. D, Posterior view; scale = 10mm.

and has been referred to the Herrerasauridae (Novas, 1992; 1994). So far no palaeobiogeographical pattern is apparent from these occurrences other than a possible faunistic link between the Southern part of Brazil and Argentina during the Triassic.

The Late Cretaceous *Antarctosaurus brasiliensis* is regarded as a titanosaurid sauropod (Arid & Vizotto, 1971), although the fragmentary nature of the type specimen makes it difficult to establish its phylogenetic position within Titanosauridae. Titanosaurid sauropods in Late Cretaceous strata of Brazil are not unexpected, since they occur widely in other parts of South America (Huene, 1929; Bonaparte, 1986; Powell, 1987; McIntosh, 1990a). Although titanosaurids have been regarded as 'typical' Gondwanan sauropods (e.g., Bonaparte, 1984), they are also reported from Europe and North America (e.g., McIntosh 1990a). This has been used to suggest that faunal interchanges between northern continents and Gondwana happened during the Late Cretaceous (e.g., Bonaparte, 1984; Buffetaut, 1989b). A better understanding of the ingroup relationships among titanosaurid taxa is needed to test this hypothesis.

The occurrence of spinosaurids from Albian strata of Brazil (Kellner, 1994a; Martill et al., 1996; Kellner & Campos, 1996) is very interesting from the palaeobiogeographical point of view. Due to the fragmentary nature of most specimens attributed to Spinosauridae, their ingroup relationships are very difficult to establish. Nonetheless, the Brazilian and some African spinosaurids (*Spinosaurus aegyptiacus* and iso-

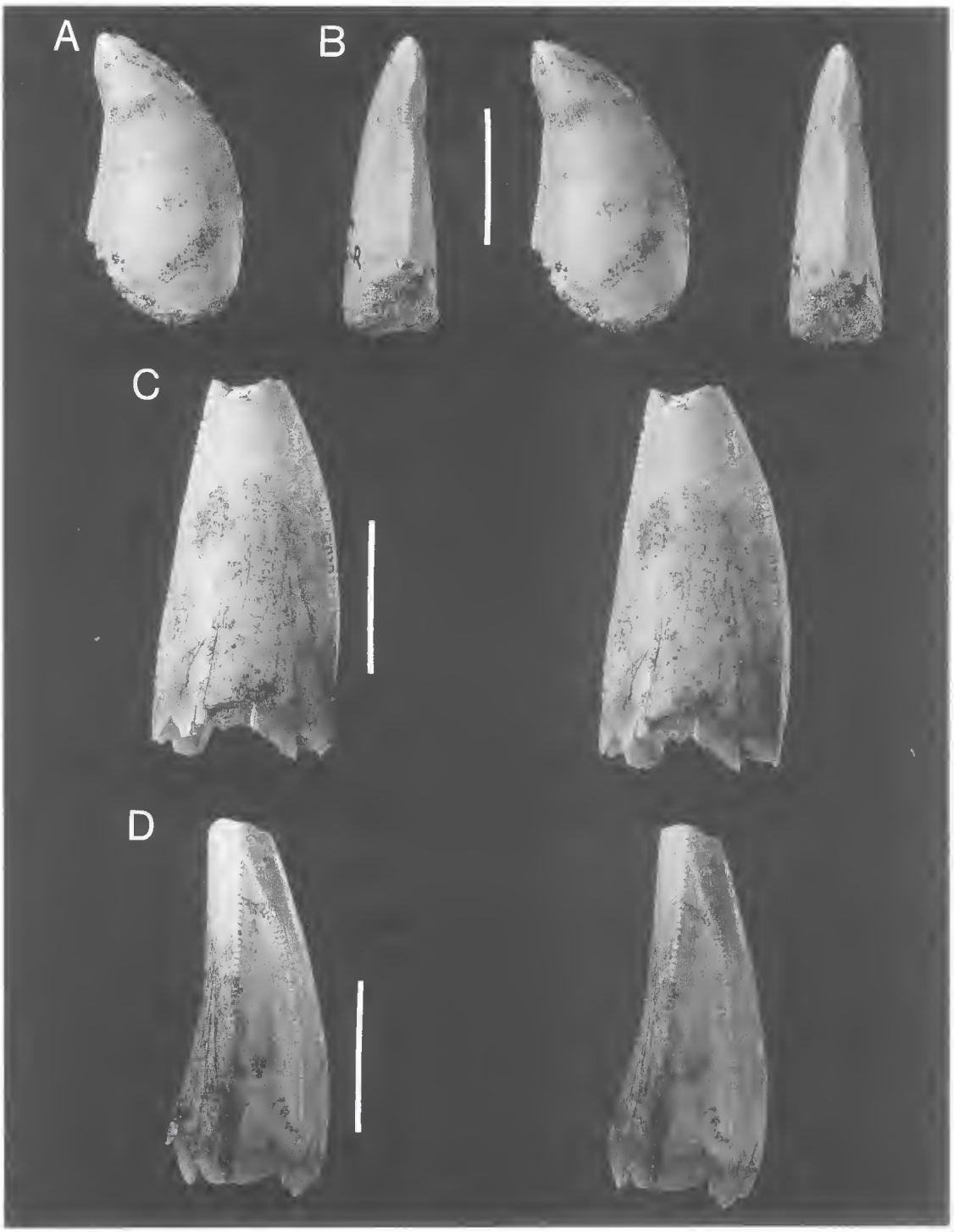

FIG. 9. A-B, Theropod tooth from the upper portion of the Late Cretaceous Bauru group. A, Stereopair of the labial view. B, Posterior view; note the irregular carina; scale = 10mm. C-D, Theropod tooth from the upper portion of the Late Cretaceous Bauru group. C, Stereopair of the lingual view. D, Anterior view; note the split carinae; scale = 10mm.

lated teeth found in Tunisia and Morocco) have developed teeth with unserrated carinae. This synapomorphic character suggests a close relationship between the Brazilian and those African spinosaurids.

Baryonyx, known only from Europe, lacks this derived dental feature. Despite the discussion whether this European taxon should be classified in its own higher taxonomic unit (i.e., Baryonychidae), there is a consensus view that *Baryonyx* and spinosaurids are closely related (Charig & Milner, 1986, 1990; Buffetaut, 1989a; Paul, 1988). The morphological features of the anterior portion of the rostrum and the particular structure of the teeth shared by *Baryonyx* and spinosaurids supports this hypothesis. I suggest that *Baryonyx* is a primitive member of the spinosaurid clade, lacking the dental character which seems to unite at least some of the Gondwanan forms.

The above phylogenetic hypothesis supports two biogeographic points:

a) that Brazilian and African spinosaurid distribution may be the result of an Early Cretaceous vicariant event (i.e., opening of the South Atlantic Ocean);

b) that the spinosaurid clade is not an exclusively Gondwanan group as previously proposed (e.g., Bonaparte, 1986; Russell, 1993), but was originally more widespread. In the middle part of the Cretaceous an apparently monophyletic group of spinosaurids occupied western Gondwana, where they diversified and eventually gave rise to the African and Brazilian taxa.

In addition, a literal interpretation of stratigraphic data suggests that dinosaur dispersal events in the Cretaceous were not only directed from Gondwana to Europe as proposed by Russell (1993), but may also have occurred in the reverse direction. All spinosaurids from Brazil and Africa are Albian or younger, while *Baryonyx*, here regarded as a primitive member of this clade, is Barremian. The limited information about the taxa mentioned, particularly regarding the African and Brazilian forms, makes the previous suggestion only a very preliminary hypothesis. Note that it is still possible that spinosaurids arose in Gondwana at an even earlier time, and that *Baryonyx* may represent a plesiomorphic lineage which migrated into Europe prior to the break-up of western Gondwana. More complete dinosaur material from Brazil and from Africa are needed to test this hypothesis.

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